The neuroanatomical organization of intrinsic brain activity measured by fMRI activity in the human visual cortex

Gravel Araneda, Nicolas Gaspar

General introduction 1

Invasive electrophysiological recordings of neuronal activity from the visual cortex of cats and other animals have revealed that spontaneous neuronal activity reflects the underlying neuroanatomical organization [30, 70, 40]. However, for non-invasive and indirect functional magnetic resonance imaging (fMRI) recordings of neuronal activity from visual cortical areas, this relationship between intrinsic activity (often referred to as "resting-state") and cortical neuroanatomical organization is not immediately obvious [42, 36, 62, 11, 27].

When measured using fMRI, intrinsic fluctuations in blood-oxygen level dependent (BOLD) activity are correlated between distant brain regions that are anatomically connected, such as homologous areas in the two hemispheres [6, 73]. For this reason, resting state (RS) fMRI has been widely used to study whole-brain interactions in health and disease [63, 72]. However, interpreting patterns of RS-fMRI activity at a more local scale (e.g., that of the visual cortex) remains challenging as activity in nearby sites can be correlated as a result of either neuroanatomical connections, or metabolic and vascular relationships [12, 47, 45, 34, 58, 46]. Currently, this uncertainty limits the use of RS-fMRI for characterizing visual cortical activity in health and disease.

A better understanding of the relationships between neuronal activity, brain anatomy and hemodynamics would help to develop RS-fMRI as a valuable tool for fundamental and applied —non-invasive— research in humans. Aiming to contribute to the understanding of these relationships, this thesis focuses on the following question: What can we learn about the neuroanatomical organization of the human visual cortex from RS-fMRI recordings?

With this central question in mind, I hypothesize that RS-fMRI activity in the human visual cortex reflects its underlying neuroanatomical organization. Using advanced anatomical MRI techniques and novel fMRI analysis methods, I will characterize and interpret the spatial and temporal organization of in-

trinsic fluctuations in BOLD activity across striate (V1) and extrastriate visual cortex (V2 and V3). Moreover, I will discuss how these fluctuations may be shaped by neuroanatomical, physiological and vascular factors.

In the following sections, I outline the questions and main findings of each experimental chapter, while in the background section, I describe the main anatomical features of the human visual system, summarize the experimental methodologies used in this thesis and briefly describe the emergence of the field of resting state research. The latter section reviews some of the previous studies that my work builds on and helps to remind that the brain is not only concerned with the demands imposed by the environment but also with internally generated dynamics. As we will see in the experimental chapters of my thesis, the neuroanatomical organization of the visual system forms a complex recurrent network of feedforward, feedback and lateral connections that cannot be fully grasped from the classical "sandwich" perspective (perception-cognition-action) of brain function [21] but perhaps —as I will discuss later (in **chapter 6**)— by a more constructivist and enactive view of brain function that accounts for recurrent neural processing and circular causality [71, 38].

1.1 Outline

This thesis comprises four experimental sections. In **chapter 2** I ask whether visuotopic organization [1] can be derived from 7T RS-fMRI activity. Based on the hypothesis that intrinsic fluctuations in BOLD activity reflect underlying neuroanatomical organization, I show that it is possible to map —based on RS-fMRI recordings— cortico-cortical neuronal interactions between V1, V2 and V3 using connective field modeling [32, 27].

Based on the hypothesis that both intrinsic and stimulus-evoked BOLD fluctuations are anchored by the same neuroanatomical connections, in **chapter 3** I ask whether patterns of synchronized fMRI activity in RS and visual field mapping (VFM) are comparable (at 7T). By examining local patterns of phase covariation, I find synchronization clusters that are similar, regardless of whether they are derived from RS or VFM data. However, in activity obtained during VFM, phase synchronization is spatially more extensive than in RS derived activity, reflecting stimulus driven interactions between local responses. Nevertheless, the resemblance between RS and VFM-derived synchronization clusters suggests that they share a common neuroanatomical origin [28].

Methods to analyse and interpret RS-fMRI activity can become valuable tools for the study of human neuronal activity in vivo, in particular if they can be generalized to different magnetic field strengths. To verify this for connective field modeling and cluster synchronization analysis of RS data, in **chapter 4** I study the feasibility of reproducing the main findings of **chapters 2 & 3** using data acquired with a 3T rather than a 7T scanner. Despite the lower resolution and signal-to-noise ratio of the 3T data, I find that the results obtained with it are in fair agreement to those obtained previously with 7T data.

[1] When the image's spatial relationships formed in the retina are preserved in the visual cortex in the form of visual field maps: nearby neurons respond to nearby locations in the image.

In **chapter 5** I ask whether the propagation of BOLD activity within and between visual field maps relates to structured neuronal activity. To explore this question, I implement a modeling approach aimed at disentangling the contributions of local activity and directed interactions in shaping BOLD activity propagation [26]. Applying this approach to 7T fMRI data reveals changes in cortical excitability and directed interactions in RS and VFM, pointing to a task-dependent reconfiguration of local, feedforward and feedback interactions across the visual system [29].

1.2 Background

In this section, I provide a general overview for those interested in studying the human visual cortex using RS-fMRI. I briefly describe the anatomical organization of the human visual system and provide some background on the field of fMRI and resting state measurements. For more detailed accounts on the neuronal and anatomical organization of the human visual cortex see e.g. [37, 74].

1.2.1 Visual pathways

Light, in the form of structured energy distributions, is transduced by photoreceptor cells in the retina (rods and cones) into electrical membrane potentials [24]. These potentials are then shaped by a recurrent cellular network consisting of bipolar, horizontal, and amacrine cells. Together they form a mosaic of functional subunits that contribute to inhibitory and sensitivity-adjustment mechanisms and communicate with the retinal ganglion cells (RGC). The axonal projections from the RGC exit the eye to form the optic nerve. These fiber projections from the two eyes decussate in the optic chiasm, with fibers from the left and right half of each retina going to the left and right hemispheres, respectively. Optic nerve fibers project primarily to the lateral geniculate nucleus (LGN), which relays to occipital visual cortical areas –the topic of the research in this thesis.

1.2.2 Retinotopic organization of the visual cortex

Shaped by evolutionary and developmental constraints, the anatomical circuitry of the human sensory cortices follows the topographic organization of their corresponding sensory surfaces. For the visual system, the result is that the image's spatial relationships formed in the retina are preserved in many regions of the cortex in the form of visual field maps: nearby neurons respond to nearby locations in the image [37]. These retino-cortical maps are said to be retinotopically organized, yet their actual location and shape is determined by different constraints from those that shape the eye [64, 55]. The topographic organization of the primary visual cortex (V1), located along the calcarine sulcus, accommodates an hemifield representation of the retinal image in which the foveal region is greatly magnified –a phenomenon called cortical magnification [65].

The nearby visual field maps V2 and V3 cluster around V1, sharing parallel eccentricity representations. However, the visual field maps in V2 and V3 are discontinuous. They split into dorsal and ventral parts, with angular representations alternating in visual field sign along the horizontal meridian. As a result, V2 and V3 are organized into two quarter hemifields. Other extrastriate visual cortical areas are organized similarly [74]. The multiplicity of visual field maps in the visual cortex appears to reflect the fact that our perceptual machinery is attuned to stable structural features in our habitat. As neurons process different aspects of the image, cortical circuitry is organized into receptive fields that preserve its spatial organization. As a result, cortical areas subserving different functions still preserve this level of organization [74]. In the experimental chapters that will follow, I relate task-dependent changes in fMRI activity to the retinotopic organization of V1, V2 and V3.

1.2.3 Hierarchical organization of the visual cortex

Traditionally, neuroanatomical connections among visual cortical areas have been thought to follow a primarily parallel-hierarchical bottom-up architecture [19]. In this view, parallel neuronal pathways, originating from anatomically and functionally distinct cell types in the retina [14], connect to thalamic and cortical structures following a precise retinotopic ordering. The visual processing of retinal signals unfolds then through a series of stages in which low-level stimulus features are processed first by 'early' visual cortices such as V1, and increasingly complex features are processed sequentially by 'higher' extrastriate visual cortices [50].

However, feedforward connections along the visual hierarchy areas are typically complemented by reciprocal feedback connections [23, 10, 41]. For example, extra-retinal inputs to V1 may arrive from extrastriate visual areas such as V2 and V3 [54, 53, 61], but also indirectly from more distant corical areas [66, 56, 20, 7, 15]. Moreover, reciprocal connections between V1 and visual thalamic structures have long been described, yet, their functional relevance is not yet fully understood [31, 35, 3, 69]. The integration of feedforward and feedback interactions along the visual hierarchy enables the modulation of ongoing cortical dynamics by incoming sensory input [25, 61]. In **chapter 5**, I will implement a generative model of directed interactions to examine the presence of state-dependent changes in the feedback and feedforward interactions between V1, V2 and V3.

1.2.4 Neurovascular coupling

In most of the visual cortex, blood is supplied by the calcarine and basilar arteries. Flowing through their ramifications, blood arrives in a network of small arterioles and capillary beds. After irrigating these capillary beds, which are arranged perpendicularly to the cortical surface, blood is drained through small venous channels into the dural venous sinuses. Neuroglia and astrocytes [59], the brain's housekeepers, regulate blood flow at the level of the capillary beds. These cells form part of the blood-brain barrier. They coordinate local blood

supply, nutrient transport and neurotransmitter release, and thus provide a crucial contribution to neuronal activity [12]. Thanks to this coupling between blood supply and neuronal activity, it has become possible to —indirectly— estimate neuronal population activity using non-invasive instruments like magnetic resonance scanners. In the next sections, I will show how fMRI has allowed to map the topographical and neuroanatomical organization of visual field maps in the human visual cortex.

1.2.5 Functional magnetic resonance imaging

In order to estimate neuronal activity patterns across early visual cortical areas I used fMRI. This technique measures changes in blood oxygenation, which has been shown to be indirectly related to neuronal activity [45]. Local neuronal activity induces changes in the ratio between oxyhemoglobin and deoxyhemoglobin, which can be detected due to their differential magnetic susceptibility [57]. This effect is named the blood-oxygen level dependent (BOLD) effect, which is the basis for fMRI. In my studies, I have used primarily 7T fMRI data. However, in **chapter 4**, I also examine 3T data. Higher magnetic field strengths allow for a better signal-to-noise ratio and spatiotemporal resolution. However, the temporal resolution of fMRI is limited by the hemodynamic response to neuronal activity, not by the magnetic field strength.

1.2.6 Retinotopic mapping using population receptive field (pRF) and connective field (CF) modeling

The development of functional magnetic resonance imaging (fMRI) has allowed to map the topographical and neuroanatomical organization of visual field maps in the human visual cortex [18]. Modeling the hemodynamic responses to hypothetical neuronal activity elicited by a stimulus allows the mapping of population receptive field properties [68]. The population receptive field (pRF) method relies on this approach [17]. The method uses a parameterized forward model of the neuronal population responses, a description of the hemodynamic response function (a two-gamma HRF model) [8], and the stimulus (here I used drifting checkerboard bars) to predict evoked BOLD activity. The population receptive field model used in this thesis corresponds to a circular Gaussian characterized by three parameters: x and y (positions in the stimuli screen), and size (σ).

To find the most likely retinotopic map, a set of candidate population receptive field models are combined with the stimulus aperture to generate predictions of the neuronal responses each candidate pRF would produce. Subsequent convolution of this predicted neuronal response with the HRF gives a set of candidate BOLD responses for each combination of pRF parameters. The pRF parameters associated with the best fitting candidate BOLD responses are then chosen to summarize the response of each fMRI recording site.

Somewhat similar to the way in which the visual field is mapped on the surface of the cortex using pRFs, CF modeling describes the neuronal interactions between different cortical visual areas in terms of spatial integration and cortical selectivity maps. CF modeling enables the characterization of a target record-

ing site (e.g. V2 and V3) in terms of the aggregate BOLD activity in a source brain area (e.g. V1), thus providing a description of the preferred locations on the cortical surface to which these target sites respond [32]. Locations in the primary visual cortex are associated with visual field positions obtained during visual field mapping (VFM). Therefore, visual field coordinates can be inferred for the target recording sites from the preferred locations in the source region, allowing the reconstruction of visuotopic maps even in the absence of a stimulus (e.g., RS). The technique is prominently used in **chapters 2 & 4**.

1.2.7 Resting state

Resting state (RS) research has become very popular in the last decades. Departing from the idea of the brain as a primarily reflexive device driven by the momentary demands of the environment [60, 67], RS studies suggest that the brain's operations are mainly intrinsic, involving the integration of slow internal and rapid sensory dynamics [75, 9, 44, 16]. From this perspective, sensory input modulates rather than 'forms' brain function [13].

Early evidence on the role of intrinsic brain activity came from studies of animal physiology and anatomy. Using decorticated cats, Brown [9] showed that rhythmic behaviours reminiscent of walking and running were still possible, even in the absence of sensory and cortical input. Intrinsic rhythms in brain activity were further found in humans. By recording scalp electrical potentials, Berger [5] found large-amplitude rhythmic fluctuations that appeared only when subjects had their eyes closed. These fluctuations were reported to occur at a rate of approximately 10 oscillations per second, what is now called the alpha frequency band [2]. Likewise, studying spontaneous electrical activity in the rabbit olfactory bulb, Adrian [1] found that the persistent activity of cells in the bulb unfolded as waves of electrical activity, even in the absence of sensory stimulation.

Despite these early findings, attempts to characterize and quantify intrinsic brain activity only gained momentum in the last two decades. Using multi-electrode recordings of retinal ganglion cells, Galli and Maffei [22] and Meister et al. [49] showed spontaneous wave-like propagation of neuronal firing prior to visual experience. These patterns were hypothesized to play a role in the development and formation of retinotopically ordered maps in the visual system [39, 48]. Later studies using large-scale neuronal recording approaches showed that both stimulus-evoked and spontaneous neuronal activity closely reflected the functional and anatomical organization of the visual cortex [4, 70, 40].

Parallel investigations in humans and non-human primates using fMRI recordings from the somatosensory cortex also indicated a link between the brain's intrinsic activity and its neuroanatomical organization [6, 73]. Moreover, using whole-brain fMRI recordings, it has been recently shown that the propagation of BOLD activity across distant brain areas reflects the transition between different behavioral states [51, 52]. This suggests a meaningful relationship between BOLD activity propagation and neuronal interactions between distant brain regions. Therefore, in this thesis, I ask whether task-dependent differences in BOLD activity between RS and VFM can also reveal relevant aspects of brain organization and activity, yet at a much more local scale. Thereby, I focus on

early cortical visual field maps, which are richly interconnected and for which regional variation in the hemodynamic response is less pronounced [33, 43].

1.3 References

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